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INFLUENCE OF DISTRIBUTION OF RAINFALL AND TEMPERATURE ON CORN YIELDS IN WESTERN IOWA [1]

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INTRODUCTION

Investigators who have examined the effect of weather on corn yields in Iowa have found little relation between yield and rainfall. Most studies have been made from State averages of rainfall and corn yields; however, in some cases smaller geographical areas, such as the county, have been used and the effect of monthly rainfall examined. Since the relation between yield and rainfall may vary with different soil or cultural conditions, it is thought that higher correlations might be found for still smaller areas, such as townships. There is also the possibility of getting slightly better correlations by lessening the intervals of time because the average effect of rainfall on yield may differ somewhat from one part of the month to another.

One of the primary objectives of this investigation was to study more in detail the relation between corn yield and the seasonal distribution of rainfall in Iowa for a uniform soil type, by using successive short intervals during the growing season. The finding of relationships for one soil type may lead to an inquiry as to how such relations vary with different soils and other natural or cultural conditions. The plan of study extended to the effect of temperature as well as of rainfall; also, to the possibility of pooling data from several locations in lieu of using data for a long series of years.

Not only are the relations between weather and corn yields of considerable scientific importance, but they may also be of value in forecasting annual yields of corn. There is an ever increasing demand for estimates of crop production, and this presupposes an estimate of yield. The demand comes from farmers, handlers, processors, and distributors of agricultural products, manufacturers and distributors of products to farmers, and banking institutions. Furthermore, fiscal, action, and service agencies of the Government must have accurate reports. In the past, estimates have been made for large geographical areas—the entire country, regions, or States. Now, estimates are needed for smaller areas, such as counties or townships, and for dates further in advance of harvest; the problem then becomes more than one of estimating what has been produced. It necessitates, at specified times during the growing season, an

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[2] The authors express their appreciation to W. G. Cochran and George W. Snedecor of Iowa State College of Agriculture and Mechanic Arts for helpful suggestions and criticisms.

appraisal of the current growing conditions jointly with crop development to that time.

It is not to be supposed that any number of studies of this nature will replace the necessity for the crop statistician. Instead, it is assumed that further information as to the importance and effect of various weather factors will help him to appraise more accurately the situations that he meets. It remains for the statistician to take the basic information and work up serviceable indications for particular areas and years somewhat in the fashion suggested by Wallace (*8*).[3] Each area and probably each year is a specific problem.

PREVIOUS INVESTIGATIONS

For the margins of the Corn Belt earlier investigators, among them Mattice (*5*), have found a number of aspects of weather (for example, July rainfall, June temperature, or accumulated degrees above 90° F.) to be related to corn yields. Hodges (*4*), studying weather and corn yields in Kansas, showed a high negative correlation between July temperatures and corn yields, and was able to build up a multiple curvilinear regression which gave a correlation of 0.9+ for certain areas of Kansas and the State as a whole. Using simple correlation methods, Rose (*6*) studied data for 55 counties scattered over the Corn Belt. At the eastern border in Ohio he observed, as had Smith (*7*) earlier, that July rainfall had a positive correlation, 0.4 to 0.6, with corn yields. June temperature was also positively correlated with corn yield. On the southern, southwestern, and northwestern margins, July temperatures and corn yields were negatively correlated. At the southern margin, there was a positive correlation between July rainfall and yield. No single climatic factor, however, gave statistically significant correlations with yield over all parts of the Corn Belt. At divergent points within the same States, Rose found given aspects of weather to be both positively and negatively correlated with yield.

For the heart of the Corn Belt Rose obtained no high correlations, and consistent patterns were lacking for many of the aspects of weather. Previously, Wallace (*8*), using similar methods, obtained about the same results and concluded that the problem of predicting corn yields from weather is relatively simple in the southern half of the Corn Belt as compared with the northern half.

As to the lack of correlation in the heart of the Corn Belt, Rose in his conclusion states, "Presumably corn yield in this core area is somewhat affected by the factors significant on the surrounding margins; but, with several factors operative—perhaps first on one, then on the other side of the optima, and thus with conditions generally favorable—variation in any one factor has little effect by itself."

A hypothetical curve representing the relationship between a weather factor and yield can be drawn. As the amount of a given aspect of weather increases, a point is reached beyond which an additional amount does not increase the yield. This point is called "optimum." In a region where near-optimum conditions prevail, a unit deviation in the weather factor has relatively little effect on yield, whereas if the weather factor varies about a point at some distance to either side of the optimum, there is a comparatively large change in yield for each unit change in the weather factor. If the given aspect

[3] Italic numbers in parentheses refer to Literature Cited, p. 545.

of weather fluctuates about a point at or near optimum, both a larger or smaller amount of the weather factor may have a diminishing effect on yield. An assumption of linearity is most nearly valid in regions where the aspect of weather always remains above or below the optimum.

With a multitude of factors affecting yield, all of which are generally not far from optimum, as is the case in Iowa, it appears unlikely that there is much correlation between yield and a given aspect of weather, such as July rainfall. At the margins of the Corn Belt the situation differs in that one or two weather factors generally remain at an appreciable distance from optimum, and hence play an important part in determining yield.

SELECTION OF DATA

As previously stated, one of the objectives is to study further the relation between yield and rainfall (and temperature) under uniform soil and cultural conditions, by using successive short intervals of time. R. A. Fisher (*2*) developed a method employing rainfall for small intervals of time. His approach, to be briefly described later, will be that of the present study.

From the annual Farm Census in Iowa there are available annual yields of corn by townships dating back to 1924, and in or near a number of townships are weather stations affording suitable weather data. For the rather complicated analysis used by Fisher a longer series than 15 or 16 years is desirable. Therefore, we examine the possibility of choosing several stations [4] and pooling the data in order to increase the number of station years. Although such a procedure is not always successful, it can be subjected to available tests.

In western Iowa it was possible to select townships from an extensive area which were alike with respect to: (1) Soil area—Missouri loess; (2) soil type—Marshall silt loam; (3) slope of land—10 percent or less; (4) percentage of land in intertilled crops—40 to 50 percent; (5) depth of soil—4 inches or over.

A wide distribution of townships was sought in order that weather might differ as much as possible in each year. Six townships and weather stations, two in each of the three western crop-reporting districts, were chosen:

Weather station:	*Township*
Rock Rapids	Rock.
Alton	Nassau.
Carroll	Maple River.
Little Sioux	Little Sioux.
Atlantic	Grove.
Corning	Jasper.

RAINFALL ANALYSIS

In Iowa early spring rains are considered beneficial to the corn crop because they build up the moisture reserve in the subsoil. From planting time through early cultivation (for 5 weeks beginning approximately May 5) rainfall is adequate in most years and possibly greater than optimum, for at that time excess rainfall might impede cultivation or be accompanied by temperatures which are too low for proper germination and development of the seedlings. From early

[4] Station refers to both the weather station and the associated township.

July to late August more than normal rainfall is generally thought to be favorable to corn growth. The greatest benefits probably accrue in late July or the first part of August when the normal rainfall is at a low level, and the transpiration surface of the plant has reached a maximum.

In view of these facts one can conceive a graph which would picture the average effect on corn yield of an inch of rain at any time between May 1 and October 1. This graph can be thought of as a smooth curve which changes rather slowly since the effect of an inch of rain would not be appreciably different if it came a day or two earlier or later. Roughly, one might expect such a curve to start with a moderate positive value, recede to a minimum around June 1, rise to a maximum near August 1, and then decrease until the end of the season. It is clear that the curve can be represented by a mathematical function of time, but how can the function be evaluated?

First, we must specify the function. For our problem a third degree equation is suitable. This may be written

$$a=\alpha_0\xi'_0+\alpha_1\xi'_1+\alpha_2\xi'_2+\alpha_3\xi'_3 \tag{1}$$

where a represents the effect of an inch of rain, the α's are constants to be determined, and ξ'_0, ξ'_1, ξ'_2, and ξ'_3 are orthogonal polynomials (*3*) (in this case orthogonal functions of time) of degrees 0, 1, 2, and 3 respectively. We shall call equation (1) the regression equation and the α's the regression coefficients.

The evaluation of the regression coefficients involves tabulation of the rainfall data by short intervals of time; in this study thirty-one 5-day intervals were used. From the rainfall data a set of quantities, ρ_0, ρ_1, ρ_2, and ρ_3, is computed for each season. These quantities are coefficients of polynomials of the form

$$\rho_0\frac{\xi'_0}{S(\xi'^2_0)}+\rho_1\frac{\xi'_1}{S(\xi'^2_1)}+\rho_2\frac{\xi'_2}{S(\xi'^2_2)}+\rho_3\frac{\xi'_3}{S(\xi'^2_3)} \tag{2}$$

fitted to the rainfall data for each season. Then, the α's are computed by the usual rules of multiple regression. The theory of this device is presented by Fisher (*2*). Equations (1) and (2) are taken from Davis and Pallesen (*1*).

The records available for this investigation afforded data for only 15 years, 1924–38. Of these 15 years, 1934 and 1936 were abnormal, yields in many townships being 5 bushels per acre or less. The poor yields were caused by long periods of very high temperature together with the lack of rainfall. This introduces some complications since the inclusion of these 2 years in the analysis could lead to statistically significant results, whereas if they were omitted different conclusions might be drawn about the influence of temperature and rainfall on yield. Thus it was thought advisable to make the analysis with all years included and then with the years 1934 and 1936 omitted.

To develop a regression for predicting differences in yield from year to year, one should use only the yearly means as proximately relevant data. But, in our case more data are desired, and it is thought that a better estimate of the regressions might be obtained by pooling the experiences at the six stations. By means of the arithmetic procedure known as the analysis of variance, the total variability in the combined data was separated into two parts; namely, the variability among

station means, and the intrastation variation, which is an average of the variability arising at each of the six stations. The first component was influenced not only by differences in weather conditions but also by variations in farm practices, average soil fertility, and other factors that could not be taken into account in selecting the townships; hence, variation among station means was excluded and the regression analysis based on the intrastation variation.

With 1934 and 1936 omitted the regression coefficients together with their standard errors are:

$$\alpha_0 = 0.1194 \quad \pm 0.1828 \qquad \alpha_2 = -0.0006108 \pm 0.002431$$
$$\alpha_1 = 0.005113 \pm 0.01819 \qquad \alpha_3 = -0.0006270 \pm 0.0003151$$

None of the α's is statistically significant except the coefficient of the cubic term, α_3, which is just at the 5-percent level. This would indicate that in general a little more rainfall than average following the middle of the season and a little less before the middle has been beneficial.

The mean effect (fig. 1) of an inch of rain more than average for any 5-day period during the season is obtained from the equation

$$a = 0.1194\xi'_0 + 0.005113\xi'_1 - 0.0006108\xi'_2 - 0.0006270\xi'_3$$

by substituting the values of the ξ''s for $n=31$. In figure 1 the x's mark the standard error of the ordinates of the curve at four different points. The large standard errors show that the average effect of rainfall on corn yield is inaccurately determined. None of the points on the curve is at a distance of more than two standard deviations from the 0 line. The nonsignificance of the regression curve is confirmed by the analysis of variance (table 1), since the value of the F ratio is only 1.4. The regression appears to be of little or no aid in estimating the yield of corn.

When 1934 and 1936 are included a statistically significant regression is obtained, the regression accounting for 29 percent of the total variation in yield. The total sum of squares, however, was increased from 3,024 to 12,224, and even though the regression was significant, the mean square of the deviations from regression was 109.0—a much larger quantity than either the corresponding mean square of 41.0 (table 1) or 42.0, the variance of the actual yields for the 13 more common years.

TABLE 1.—*Rainfall regression analysis based on the intrastation variation, 1924–38 (1934 and 1936 omitted)*

Source of variation	Degrees of freedom	Sum of squares	Mean square	F
Regression	4	232	58.0	1.4
Deviations from regression	68	2,792	41.0	
Total	72	3,024	42.0	

The intrastation variation is actually a weighted average of the variation among yearly means and the station by year interaction; i. e., the variation at the stations after allowing for differences in the yearly means and differences in the station means. Thus, the regression based on the intrastation variation is a weighted mean of two

regressions, one based on the variation among years and the other on the station by year interaction. Ordinarily, to predict difference from year to year one would use the regression among years. In case the regression among years and the regression based on interaction differ significantly, the intrastation regression would not be appropriate for estimating differences in yield from year to year. It will be pointed out later that the mean square of the deviations from the intrastation regression (41.0 in table 1) is very likely to give a negatively biased estimate of the error mean square for estimating

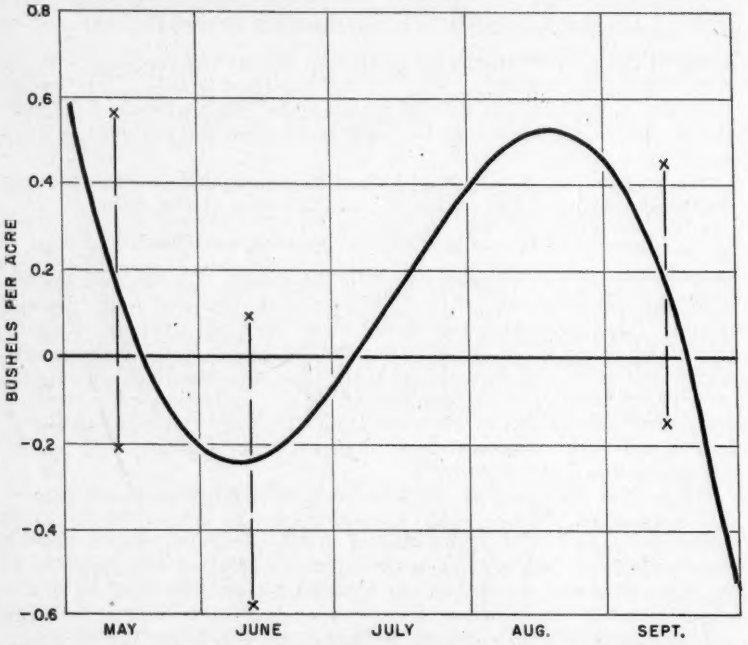

FIGURE 1.—Mean effect of an inch of rainfall above average on the yield of corn in western Iowa.

yearly differences. These points will be examined in the temperature analysis. For the case of rainfall such a study is probably not worth while.

TEMPERATURE ANALYSIS

In the area under investigation it is believed that high temperature frequently has a harmful effect on the yield of corn. To discover the effect of high temperature, maximum daily temperature has been used rather than the mean or minimum. The temperature data were handled in the same manner as those of rainfall. In place of total rainfall for 5-day periods we now have 5-day averages of daily maximum temperatures.

When the regression is based on intrastation variation including 1934 and 1936, the coefficients, α's, and their standard errors are:

$$\alpha_0 = -0.04472 \pm 0.01103 \qquad \alpha_2 = 0.001768 \pm 0.0^3 3806$$
$$\alpha_1 = 0.004060 \pm 0.001591 \qquad \alpha_3 = 0.0^3 1823 \pm 0.0^4 3713$$

All the coefficients are statistically significant.

The regression curve (fig. 2) is the graph of

$$a = -0.04472\xi'_0 + 0.004060\xi'_1 + 0.001768\xi'_2 + 0.0^3 1823\xi'_3$$

As indicated by the rather small standard deviations of the ordinates, the curve is fairly well determined (fig. 2). From the third week

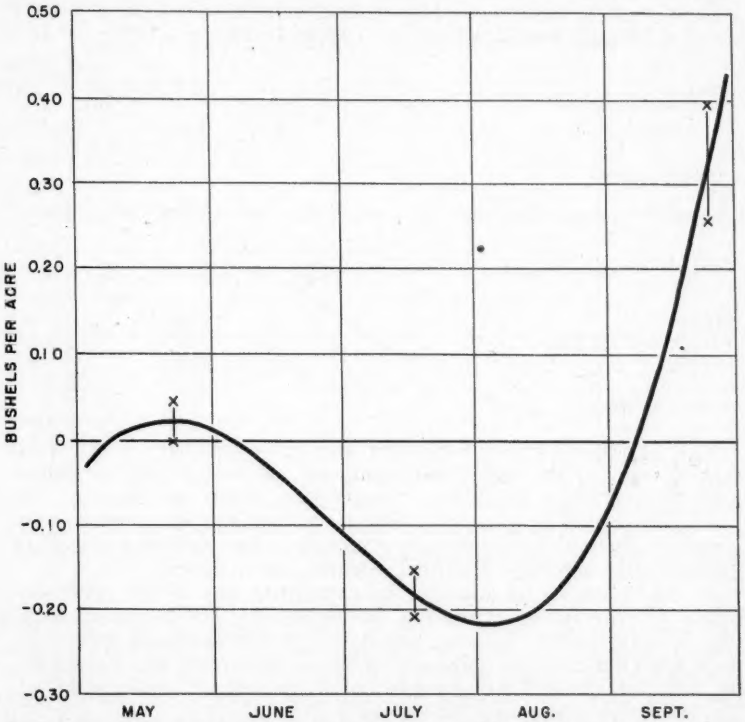

FIGURE 2.—Mean effect of a degree of maximum temperature above average on the yield of corn in western Iowa.

of June to the first of September the curve shows that more than average [5] maximum temperature decreases the yield of corn. Before the middle of June the effect is relatively small. High temperatures during the latter part of September are evidently beneficial to corn. The effect, however, as shown by the curve is probably exaggerated. Perhaps a better picture could be obtained by extending the ending date about 2 weeks and fitting a fourth degree polynomial. One would then expect the curve to reach a maximum some time around October 1.

[5] The average is established on the basis of the 15 years.

From the analysis of variance (table 2) we see that the regression is highly significant, and accounts for 58 percent of the total variation. The situation here is similar to that for rainfall. When 1934 and 1936 are omitted the F ratio drops from 27.7 to 3.8 (table 3), but the regression is still highly significant. Hence in more normal years the existing variations in temperatures in western Iowa usually exert a greater effect on corn yield than the existing fluctuations in rainfall.

TABLE 2.—*Temperature regression analysis based on intrastation variation, 1924–38 (1934 and 1936 included)*

Source of variation	Degrees of freedom	Sum of squares	Mean square	F.
Regression	4	7,100	1,775**	27.7
Deviations from regression	80	5,124	64.0	
Total	84	12,224		

**Highly significant.

TABLE 3.—*Temperature regression analysis 1924–38 (1934 and 1936 omitted)*

Source of variation	Degrees of freedom	Sum of squares	Mean square	F.
Regression	4	556	139**	3.8
Deviations from regression	68	2,468	36.3	
Total	72	3,024		

**Highly significant.

The regression curve with 1934 and 1936 omitted (fig. 3) shifts upward and to the right, shortening the period of time for which more-than-average maximum temperature tends to decrease the yield. It should be remembered that in this case the average temperatures during the season are generally a few degrees lower since 2 years with extremely high temperatures are excluded.

At this point let us examine the appropriateness of the regression based on intrastation variation for estimating differences in yield from year to year.[6] To learn about this, the intrastation differences were analyzed into two parts, differences among years and the station by year interaction. A regression based on each part was computed. The α's for the regression among years are:

$$\alpha_0 = -0.03746 \pm 0.2675 \qquad \alpha_2 = 0.002028 \pm 0.0^3 9951$$
$$\alpha_1 = 0.004752 \pm 0.003795 \qquad \alpha_3 = 0.0^3 1846 \pm 0.0^4 8712$$

whereas those for the regression based on interaction are:

$$\alpha_0 = -0.09106 \pm 0.02294 \qquad \alpha_2 = 0.01039 \pm 0.0^3 4850$$
$$\alpha_1 = 0.002553 \pm 0.004130 \qquad \alpha^3 = 0.0^3 1831 \pm 0.0^4 8709$$

Differences between the various pairs of corresponding coefficients were tested, but none was found to be statistically significant. Hence the two regressions seem to be in close enough agreement to justify

[6] The discussion from here on refers to the case with 1934 and 1936 included.

the procedure of pooling the data and using the average regression (based on the intrastation variation), which supposedly gives a better estimate of the true regression coefficients. Agreement between the two curves is shown in figure 4.

The analyses of variance for the regression among years and the regression based on interaction are given in tables 4 and 5 respectively. It is of importance to note that even though the average regression may be legitimate, the error mean square from table 2 underestimates the error variance for estimating yearly differences because of the intrayear correlation between the station yields. In table 4 the sums of squares are six times those that would be obtained if one actually used the 15 yearly means; hence, the standard error associated with

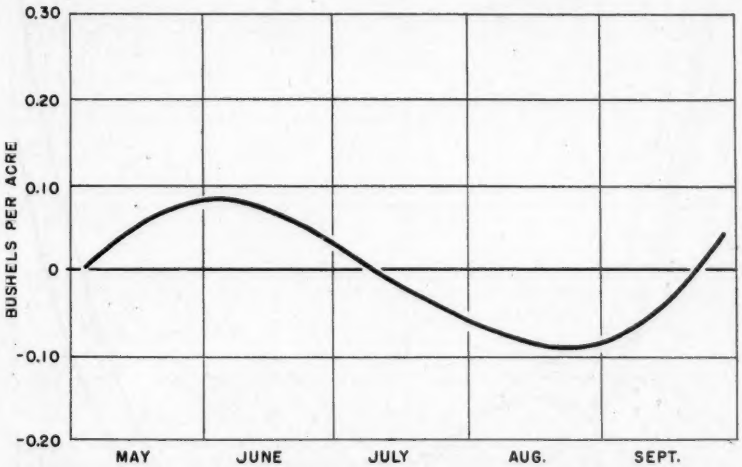

FIGURE 3.—Average effect of maximum temperature—1934 and 1936 omitted.

an estimate of the yearly mean yields for the six stations using the regression among years is $\sqrt{321/6}=7.3$ bushels. If one uses the average regression to estimate differences among the same 15 yearly means, a standard error of 6.7 is obtained. This is considerably higher than the incorrect estimate, $\sqrt{64.0/6}=3.3$, resulting from the use of the error mean square in table 2.

TABLE 4.—*Temperature regression analysis based on variation among years, 1924–38*

Source of variation	Degrees of freedom	Sum of squares	Mean square	*F.*
Regression	4	6,315	1,579*	4.9
Deviations from regression	10	3,207	321	
Total	14	9,522		

*Significant.

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TABLE 5.—*Temperature regression analysis based on interaction, 1924–38*

Source of variation	Degrees of freedom	Sum of squares	Mean square	*F.*
Regression	4	949	237**	8.9
Deviations from regression	66	1,753	26.6	
Total	70	2,702		

**Highly significant.

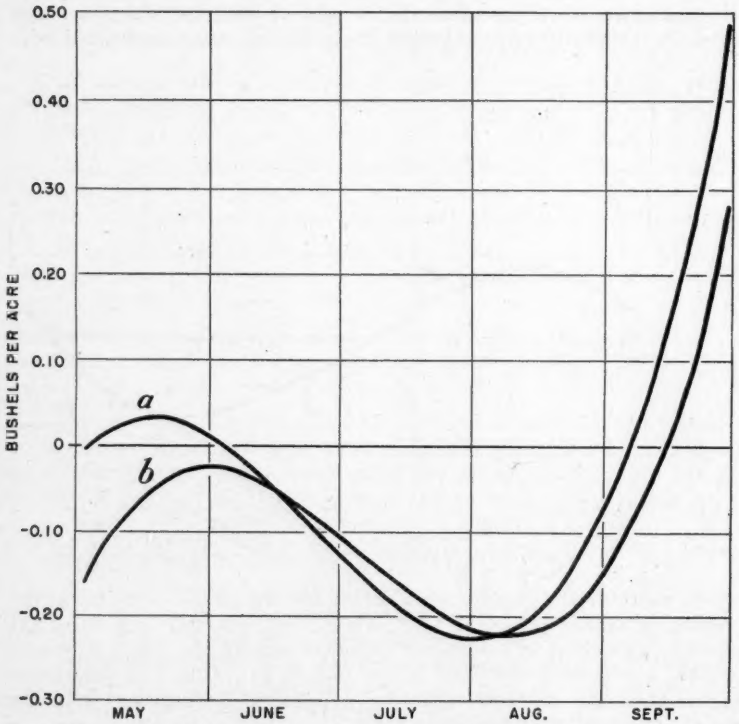

FIGURE 4.—Curves corresponding to the regression among years *a*, and the regression based on interaction (*b*).

The regression curve in figure 2 is an average of the six curves for the individual stations. If these six curves should differ by a considerable amount, one could do better from the prediction point of view by using the appropriate station curve. To check on this point, a separate analysis was computed for each of the six stations (table 6). From table 7 we note that the mean square for differences among the regressions, 33.1, is small in comparison to 74.3, the average mean square for deviations from individual regressions. Hence, from the prediction point of view, there is probably nothing to be gained by using individual regressions (fig. 5) instead of the average regression.

The six curves are much alike, and there is no apparent tendency for them to be arrayed either according to the average yield for each station or by location of the station.

Suppose there were two neighboring townships, A with a high mean yield and B with a low mean yield. For a given date one might expect the magnitude of the effect of temperature on yield to be greater for township A than township B; i. e., as the mean yield increases, the regression curve may become more pronounced. If the

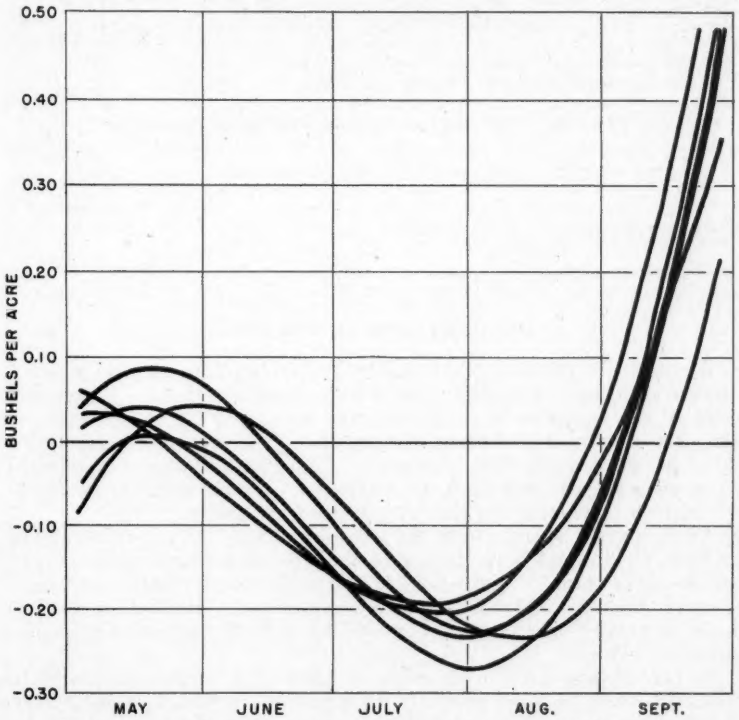

FIGURE 5.—Maximum temperature curves for the individual stations.

effect of maximum temperature at any given date is approximately proportional to the mean yield, one could obtain a single regression curve, stating the effect as a percentage of the average yield, that would be applicable to different areas which have about the same average weather conditions even though the mean yields of these areas differ. The average yields at the six stations, in the same order as in table 6, for the 15 years studied are 31.3, 33.8, 38.3, 34.0, 34.9, and 32.9. The range of the means is rather small for purposes of trying out the above idea. Since only a very small amount of additional clerical work was needed, such a regression was computed for the six stations. In this case the F ratio was 29.7 as compared with 27.7 in table 2.

TABLE 6.—*Temperature regression analysis for each station, 1924–38*

Station	Mean square		
	Regression (4 degrees of freedom)	Deviation from regression (10 degrees of freedom)	F [1]
Rock Rapids	208	61.3	3.4
Alton	338	58.3	5.8
Carroll	303	92.5	3.3
Little Sioux	257	85.0	3.0
Atlantic	428	57.4	7.4
Corning	406	91.5	4.4

[1] F at the 5-percent level for degrees of freedom 4 and 10 is 3.5.

TABLE 7.—*Differences among individual station regressions*

Source of variation	Degrees of freedom	Sum of squares	Mean square
Deviations from average regression within stations	80	5,124	64.0
Deviations from individual station regressions	60	4,461	74.3
Difference between regressions	20	663	33.1

SUMMARY AND CONCLUSIONS

By using the method developed by Fisher (*2*), corn yield in western Iowa was related to rainfall and maximum temperature. Practically none of the variation in corn yield was accounted for by variation in the amount and distribution of rainfall. Yield was more closely related to temperature than to rainfall. The standard deviation of yield from year to year was 10.6, as compared with the standard error of estimate 6.7, when using the temperature regression.

At the outset of this study the question of how the effect of rainfall on corn yield might differ from one soil type (or cultural condition) to another was raised. Since the correlation between rainfall and yield is small, such a study would appear unprofitable. Rainfall in western Iowa is usually near optimum except for part of the time when temperature is high.

In lieu of data for a long series of years at a single location, data from six locations were pooled. This procedure gave a suitable estimate of the temperature-regression equation, but produced an underestimate of the error for estimating differences from year to year. The reason for the underestimate of error was the intrayear correlation between the station yields.

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RESISTANCE OF TOBACCO TO BACTERIAL WILT (BACTERIUM SOLANACEARUM) [1]

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INTRODUCTION

The bacterial wilt or Granville wilt (*Bacterium solanacearum* E. F. Smith, syn. *Phytomonas solanacearum* (E. F. Smith) Bergey et al.) is a common and serious disease of flue-cured tobacco (*Nicotiana tabacum* L.). It is extremely destructive in north-central North Carolina, where, on about 75,000 acres of sandy soil (mostly of the Granville type) is produced tobacco of exceptionally fine body, aroma, and color. Bacterial wilt has materially reduced the value of this land. For example, land free of wilt in this area would find ready sale at $100 an acre, while the price of badly contaminated land is now about $25 an acre. This land will grow many other crops, but because of the low fertility level, it is not profitable to grow these crops in competition with other areas. Sandy loam types of soil of the Granville, Durham, Norfolk, and Marlboro series are most seriously affected by wilt.

The wilt desease has now been known for about 60 years, but despite careful investigations in this country from 1903 to 1917 and similar studies in the Netherlands East Indies and Japan over a much longer period, no adequate method of control has been developed, and growers in seriously affected areas regularly lose 20 percent or more of their tobacco crop from wilt.

Breeding for resistance was one of the first methods of control suggested. In 1903, Stevens and Sackett (*6*) [2] said: "The greatest hope for the redemption of land now affected lies in the development of a variety of tobacco that can resist the disease." However, these investigators concluded their work without finding such a tobacco. In 1917, Garner et al. (*1*), reporting on wilt-control investigations, said that, after testing all available foreign and domestic varieties, none was found that possessed sufficient resistance to be worth while. In view of these findings active breeding work was discontinued.

In the Netherlands East Indies, work on wilt resistance has been reported by various investigators, including Honing (*2*), Vriend (*7*), Palm (*5*), Kuijper (*4*), and Koenig and Rave (*3*). It was early observed that the Sumatra variety of tobacco was at least as resistant as any and more resistant than most varieties. Hence, various workers have sought to increase this resistance by selection. However, this work has not met with much success; the degree of resistance so far secured is not sufficient to give protection under severe disease conditions.

Work by the Bureau of Plant Industry, United States Department of Agriculture, in cooperation with the State of North Carolina, was

[1] Received for publication April 15, 1942. Cooperative investigations of the Division of Tobacco Investigations, Bureau of Plant Industry, U. S. Department of Agriculture, the North Carolina Agricultural Experiment Station, and the North Carolina Department of Agriculture.

[2] Italic numbers in parentheses refer to Literature Cited, p. 554.

resumed in 1934. It seemed probable that available gene material had been rather thoroughly studied; therefore the first step in the investigations here reported was to secure new and more extensive collections. The chief emphasis was placed on *Nicotiana tabacum*, although some attention was given to other species of *Nicotiana*.[3] Many new collections of this species were obtained by special collectors [4] in Mexico and in Central and South America.

METHODS OF TESTING

Preliminary work was conducted in the greenhouse. Plants were grown and transplanted individually into 4-inch pots—10 plants per lot. When the plants were growing rapidly, holes were punched into the soil with a sharp stick to break some of the roots. These holes were then filled with inoculum consisting of broth cultures of the bacteria, diluted about 10 to 1. Critical tests could be conducted only during the warmer parts of the year, from June to October, inclusive. During the years 1934–38, 1,034 collections were tested in the greenhouse, some two or three times, and single-plant selections were made from all of the more promising strains. After greenhouse elimination the surviving strains were tested in the field at Creedmoor, N. C., on land so heavily infected that all susceptible tobacco was usually dead by midseason (fig. 1, *A*). Except for the wilt, however, the land used was capable of producing excellent crops of high-quality tobacco (fig. 1, *B*). A total of 129 introductions were subjected to careful field test during the period 1935–41. The more promising strains have been tested many times, under widely varying conditions. It has not been deemed advisable to draw definite conclusions on any genotype with less than 3 years of experimentation, as a single year's results on wilt resistance have sometimes proved very misleading.

RESULTS

RESISTANCE OF VARIOUS SPECIES OF NICOTIANA TO BACTERIAL WILT

The following species of tobacco have been tested and found highly susceptible: *Nicotiana acuminata* (Grah.) Hook., *N. alata* Link and Otto, *N. attenuata* S. Wats., *N. caesia* Suksd., *N. cavanillesii* Dun., *N. debneyi* Domin, *N. exigua* H.-M. Wheeler, *N. glauca* Grah., *N. glutinosa* L., *N. goodspeedii* H.-M. Wheeler, *N. gossei* Domin, *N. langsdorffii* Weinm., *N. longiflora* Cav., *N. maritima* H.-M. Wheeler, *N. megalosiphon* Heurck and Muell.-Arg., *N. miersii* Remy, *N. nesophila* Johnst., *N. nudicaulis* S. Wats., *N. paniculata* L., *N. plumbaginifolia* Viv., *N. quadrivalvis* Prush,[5] *N. raimondii* Macbride, *N. repanda* Lehm., *N. rotundifolia* Lindl., *N. rustica* L., *N. stocktoni* Brandeg., *N. sylvestris* Speg., *N. tomentosa* Ruiz and Pav., and *N. trigonophylla* Dun. All these species were at least as susceptible as ordinary varieties of *N. tabacum*, so there has appeared little reason to look for resistance to bacterial wilt among the wild relatives of cultivated tobacco.

[3] These were largely obtained from Dr. T. H. Goodspeed, of the University of California.

[4] Dr. W. A. Archer and R. Stadelman, of the Division of Plant Exploration and Introduction, Bureau of Plant Industry, U. S. Department of Agriculture.

[5] This material was received under the name *N. bigelovii*. The name *quadrivalvis* antedates *bigelovii* and was used originally to describe one form of this species; hence under present rules of nomenclature it must be applied to the species as a whole.

FIGURE 1.—*A*, Tobacco crop, planted on land heavily infected with bacterial wilt, completely destroyed; *B*, a nearby crop, planted and fertilized in the same manner as that in *A*, shows the growth of tobacco that could have been produced on the land shown in *A* had it not been for the wilt.

With over 1,000 new seed collections available, the writer began work in 1934 and soon found various strains that were more or less resistant. The experience of previous investigators that strains may appear quite resistant one year and later, under more severe conditions, go down before the disease almost completely, was repeatedly duplicated. However, by 1938 the available material had been quite well covered, and the truly resistant strains began to stand out clearly. By 1940, constant elimination had reduced the resistant strains to a very compact group; the susceptibility of these different genotypes to wilt is shown by table 1.

TABLE 1.—*Resistance of various strains of tobacco to bacterial wilt, Creedmoor, N. C., 1940*

Strain	Amount of disease [1]								
	Block [2]								Mean [3]
	1	2	3	4	5	6	7	8	
Cash (susceptible control)	[4] 100	95	100	90	87.5	97.5	90	82.5	92.8
Davis Special	92.5	92.5	90	95	57.5	60.5	57.5	72.5	77.2
T. I. 79A	40	50	32.5	55	35	22.5	20	30	35.6
Xanthi	30	37.5	27.5	20	25	15	20	15	23.8
79–X [5]	20	25	25	10	32.5	5	5	5	15.9
T. I. 448A	7.5	15	12.5	12.5	12.5	12.5	10	27.5	13.8

[1] 100=maximum of disease (all plants dead); 0=no disease.
[2] Blocks 1 to 4, after tobacco; infection very heavy. Blocks 5 to 8, after corn; infection moderately heavy.
[3] Siginficant difference between means at 5-percent level, 9.4; at 1-percent level, 12.5.
[4] Approximately 50 plants per plot.
[5] F_4 from a cross of T. I. 79A and Xanthi.

Table 1 brings out important points in connection with resistance to bacterial wilt. In blocks 5 to 8, Davis Special was distinctly more resistant than the Cash control. These plots were on moderately infected land, since it had been cropped to corn the year previous. In blocks 1 to 4, Davis Special was no more resistant than the Cash control. These plots were on heavily infected land that had produced a diseased crop of tobacco the previous year. It has been a common observation that slightly wilt-resistant genotypes, such as Davis Special, show up to advantage under less severe wilt conditions. For example, they may appear quite resistant early in the summer and later be just as badly affected by wilt as ordinary susceptible tobacco. T. I. 79A and Turkish Xanthi have both displayed considerable wilt resistance. As table 1 shows, they were consistently much superior to Davis Special. A cross between these two yielded 79–X, which was more highly resistant than either of the parent strains. T. I. 448A was another highly resistant strain and possessed other very desirable characters, as will be noted later. The ability of these two strains to grow normally on wilt-infected land is illustrated in figure 2.

In table 2, data are given for four separate single-plant selections of T. I. 448A and 79–X.

As the complete destruction of the Gold Dollar control in 1941 indicates, wilt was very severe that year. Under these conditions both Xanthi and T. I. 79A were severely affected. On the other hand, T. I. 448A and 79–X strains show no more wilt than in 1940. Approximately 92 percent of the plants of both resistant strains were alive and

FIGURE 2.—Tobacco growing on the heavily wilt-infected land shown in figure 1, *A*. The row of ordinary susceptible tobacco (Jamaica) in the center has been completely destroyed. T. I. 448A (left) and a T. I. 79A–Xanthi hybrid (right), two highly wilt-resistant strains, are growing normally.

growing vigorously on September 12, 1941, and essentially the same results were obtained in 1939 and 1940. It is questionable whether significant differences exist between the different selections. These and similar data suggest that both T. I. 448A and 79–X were essentially homozygous for resistance. Both these genotypes have been thoroughly tested over a 3-year period without any indication of a break-down in their resistance, even during the very severe wilt year of 1939. A summary of the pertinent data regarding the resistant strains follows.

TABLE 2.—*Resistance of various strains of tobacco to bacterial wilt, Creedmoor, N. C., 1941*

Strain	Amount of disease [1]				
	Block—				Mean [2]
	1	2	3	4	
T. I. 448A–1	[3] 6	10	18	20	13.5
T. I. 448A–2	12	6	15	25	14.5
T. I. 448A–3	19	20	13	32	21.0
T. I. 448A–4	13	1	5	6	6.2
79–X–1	23	13	28	13	19.2
79–X–2	8	10	14	18	12.5
79–X–3	7	2	16	16	10.2
79–X–4	10	16	10	13	12.2
Xanthi	28	40	65	54	46.8
T. I. 79A	64	78	84	55	70.2
Gold Dollar (susceptible control)	100	100	100	100	100.0

[1] 100=maximum of disease (all plants dead); 0=no disease.
[2] Significant difference between means at 5-percent level, 11.9; at 1-percent level, 16.1.
[3] Approximately 45 plants per plot.

STRAINS HAVING SLIGHT WILT RESISTANCE

Strains having slight wilt resistance are typified by Davis Special (table 1) and a considerable number of foreign collections. They often showed quite striking evidences of resistance under mild conditions, but under severe conditions appeared as completely susceptible

Certain of these genotypes, having good flue-cured quality, give indications of value for crossing with the more highly wilt-resistant strains. They have no value for crossing with susceptible genotypes, as the resistance has proved both inadequate and impossible to recover in full.

Strains Having Moderate Wilt Resistance

The best strains having moderate wilt resistance were T. I. 79A and Turkish Xanthi. Most Turkish varieties were not wilt-resistant. Both T. I. 79A and Turkish Xanthi had very small leaves, and the great majority of the selections from crosses made between these and flue-cured varieties also had small leaves. In fact, the general type of these progenies has been uniformly poor, and in addition it has proved very difficult to recover full resistance after a cross to susceptible tobacco. The only really valuable result from the work with these strains has been strain 79–X (tables 1 and 2), which was selected out of the cross T. I. 79A × Xanthi.

Strains Having High Wilt Resistance

There are two strains having high wilt resistance, namely, 79–X, just referred to, and T. I. 448–A. Both have shown less than 10 percent of plants actually killed by wilt over a 3-year period of testing under disease conditions so severe that ordinary tobacco was 100 percent destroyed.

79–X is a poor plant type, but a study of both genetic behavior and pathological reactions indicates that the resistances of 79–X and T. I. 448A are basically different and are probably controlled in major part by different genes. Consequently, just as the highly wilt-resistant 79–X was obtained by crossing two moderately resistant strains that had different types of resistance, so it seems possible that a completely wilt-immune genotype may be obtained from a crossing of 79–X and T. I. 448A. This would be a useful strain to have in reserve.

Discussion of T. I. 448A has been left until last, as of all the 1,034 collections tested, this is the only one that seems likely to provide a practical solution to the problem of bacterial wilt control. T. I. 448 was obtained in Tolima, Colombia, and was labeled by the collector as a mixture of Castillo negro, Castillo blanco, and Pina. From greenhouse plantings of T. I. 448 a single plant was selected that appeared highly resistant to both bacterial wilt and mosaic. A plant of the T. I. 448A strain is shown in figure 3, *A*, and a plant of Gold Dollar, a flue-cured type, in figure 3, *B*. Plant measurements of these two are given in table 3.

The differences in general plant shape are clearly shown in figure 3. The data in table 3 indicate that T. I. 448A has more and shorter leaves than flue-cured tobacco. However, T. I. 448A did cure-out to a fair quality and proved neutral with respect to aroma. Of greater importance is the fact that numerous F_3 lines from T. I. 448A × flue-cured, grown in the field in 1941, gave a cured leaf that strongly resembled flue-cured tobacco, and some possessed the full resistance of the T. I. 448A parent. Hence, while it is not the purpose of this paper to report on the breeding work, it can be noted that satisfactory wilt-resistant flue-cured tobaccos are now definitely in prospect.

TABLE 3.—*Plant measurements of T. I. 448A and flue-cured tobacco*

Measurement	T. I. 448A				Flue-cured			
	Plant—			Mean	Plant—			Mean
	1	2	3		1	2	3	
Height.....inches..	60	60	60	60	64	60	66	63.3
Leaves.....number..	28	26	27	27	23	23	23	23
Leaf length [1].....inches..	21	20.3	21.7	21	22.3	23	26	23.8
Leaf breadth [1].....do....	11	10.3	11.7	11	12.7	11.5	13.7	12.6

[1] Maximum.

A very interesting aspect of the resistance of T. I. 448A to wilt concerns the early- and late-season behavior of this type. Early in the summer a considerable percentage of the young plants often showed wilt symptoms. Less than 10 percent died of the wilt, and practically all the deaths occurred in this early period. T. I. 448A plants showing early-season symptoms were labeled and observed throughout the summer. The great majority recovered and grew normally, with the result that during midsummer and late summer wilt symptoms were difficult to find. On the other hand, with such types as T. I. 79A, many large plants approaching maturity often wilted and died.

FIGURE 3.—*A*, T. I. 448A, a highly wilt-resistant strain that grows vigorously and has leaves of good size; *B*, Gold Dollar, a typical flue-cured variety. (Note the conical shape of plant and the "stand-up" type of leaf growth.)

SUMMARY

Search for resistance of tobacco (*Nicotiana tabacum*) to bacterial wilt (*Bacterium solanacearum*) was begun in 1934.

None of the wild *Nicotiana* species tested showed resistance.

Of 1,034 collections of *Nicotiana tabacum*, obtained chiefly in Mexico and in Central and South America, a very few showed resistance.

By crossing T. I. 79A and Turkish Xanthi, two moderately resistant strains, a highly resistant genotype, 79–X, was developed, but it was a very poor type of tobacco.

A highly wilt-resistant collection of good type, T. I. 448A, was obtained from Colombia. Over a 3-year period this strain always showed less than 10 percent mortality, even though disease conditions were so severe that susceptible tobacco was 100 percent destroyed.

T. I. 448A was also highly resistant to common tobacco mosaic.

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EXTENT OF PATHOGENICITY OF HYBRIDS OF TILLETIA TRITICI AND T. LEVIS[1]

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INTRODUCTION

The demonstration of heterothallism and hybridization in *Tilletia tritici* (Bjerk.) Wint. and *T. levis* Kühn by Flor (*2*)[2] in the United States was confirmed by Hanna (*3*) in Canada and Becker (*1*) in Germany. Each of these workers presented evidence of the heritability of chlamydospore morphology, the smooth spore character of *T. levis* apparently being dominant over the reticulate character of *T. tritici*. Furthermore, Becker (*1*) obtained some evidence of the inheritance of pathogenicity in crosses between two races of *T. tritici*. In his studies of two hybrids the inheritance of pathogenicity was found to be intermediate in one and recessive in the other, as indicated by the reaction of the highly susceptible variety, Panzer. In 1938 the writer (*4*) presented evidence of the inheritance of chlamydospore characteristics and pathogenicity in a cross between *T. tritici* and *T. levis*. A pathogenically distinct race of *T. tritici*, derived from this cross, had the pathogenic factors of both parents, and it was observed that the reticulate character was dominant. In a more recent report (*6*) evidence was presented to show that pathogenicity factors may be inherited transgressively. The purpose of this paper is to present the results of extensive studies on the pathogenicity of species and race hybrids through several generations. No consideration will be given to the inheritance of chlamydospore characteristics.

MATERIAL AND METHODS

Races T–8, T–9, T–10, and T–12 of *Tilletia tritici* and L–7 and L–8 of *T. levis* were used in these investigations. These races are designated by the numbers assigned to them by Rodenhiser and Holton (*7*). All cultures used for inoculation purposes were of monosporidial origin and were obtained by isolating single primary sporidia from the promycelia of germinating chlamydospores. Inoculations with cultures were made by the method described by the writer in 1938 (*5*), while inoculations with chlamydospores were made by dusting the seed at the rate of 0.5 gm. of spores to 100 gm. of seed. The hybrids are designated by number and are pedigreed as to race, chlamydospore, and sporidium.

Hindi (C. I.[3] 8454), a highly susceptible variety of spring wheat (*Triticum aestivum* L.), was used for the culture inoculations, and the F_1 inoculum of all hybrids was obtained from this variety. The

[1] Received for publication June 5, 1942. Cooperative investigations of the Division of Cereal Crops and Diseases, Bureau of Plant Industry, U. S. Department of Agriculture, and the Washington Agricultural Experiment Station.

[2] Italic numbers in parentheses refer to Literature Cited, p. 563.

[3] C. I. refers to accession number of the Division of Cereal Crops and Diseases.

winter wheat host testers (7) were used for the pathogenicity tests with hybrid chlamydospores, and the inoculum of segregating generations was selected from one or more of these varieties. The seed of all varieties was rendered smutfree by treating it with formaldehyde solution (1:320) for 5 minutes, after which it was thoroughly washed in running water. All inoculated seed was planted at Pullman, Wash., under environmental conditions presumably favorable for infection.

The smut percentages were determined on the basis of total heads of wheat in a 5- or 6-foot row, the number ranging from 100 to several hundred, depending upon variety, soil, and season. The smut percentages were recorded in whole numbers, fractions of one-half or more being considered whole numbers and those of less than one-half being disregarded.

EXPERIMENTAL RESULTS

Results have been obtained from studies on 50 hybrids, 23 of which resulted from crosses between *Tilletia tritici* and *T. levis* and 27 from crosses between races within these species. Of the 23 interspecies hybrids, 19 proved capable of perpetuating themselves while 4 were nonpathogenic on the host varieties used, and of the 27 interrace hybrids, 16 survived several generations of propagation and 11 were nonpathogenic. As yet, no adequate explanation can be offered for the failure of some of these hybrids to survive. In some cases it appeared to be due to failure of the spores to germinate. In other cases, however, germination of the spores was observed but no infection or very slight infection was obtained. Apparently hybrid sterility due to wideness of the crosses is of no great significance in this connection, since there was a greater degree of the nonsurvival quality in the race hybrids than in the species hybrids. Furthermore, certain selfed lines exhibited similar characteristics. Six inbred lines of L–8 and 2 of T–11 could not be propagated beyond the first generation, whereas 6 inbred lines of T–6 and 1 of L–7 were maintained through several generations without any diminution in pathogenicity. Apparently, therefore, there is no correlation between the taxonomic relationship of the parents and the survival quality of hybrids between species and between races of the wheat bunt fungi. It seems significant, however, that the majority of such hybrids can be propagated as readily as their parents and in many instances give rise to new pathogenic types.

SPECIES HYBRIDS

The percentages of smut produced by hybrids between L–8 and T–9 are presented in table 1, along with the host reaction to the parent races.[4] Table 1 shows the susceptibility of Oro to race L–8 and its resistance to race T–9, in contrast to the resistance of Hohenheimer to L–8 and its susceptibility to T–9. All of the hybrids between these two races have been tested through the sixth generation, and it appears that at least three types of pathogenicity are represented in the four hybrids listed. Hybrid 35 appeared to be identical in pathogenicity with the L–8 parent, and it also resembled this parent in having smooth spores. Two other hybrids between these two races,

[4] The host reactions to the parent races shown in tables 1 to 3 were obtained over a period of 5 years or longer.

not listed in table 1, were identical with Hybrid 35. Hybrid 38, which had reticulate spores, was unlike either parent in pathogenicity, since it was able to infect only Hybrid 128. On the other hand, Hybrid 39, which also had reticulate spores, appeared to possess a combination of pathogenicity factors from both parents, since it infected both Oro and Hohenheimer. This hybrid is similar to the one described in 1938 (*4*). Hybrid 40, through the fifth generation, appeared to be distinctly less virulent than either parent on all of the varieties, including the susceptible variety Hybrid 128. In the sixth generation, however, it exhibited a high degree of virulence on Hybrid 128 and Oro, thus resembling Hybrid 35 and the L–8 parent. However, unlike L–8, the chlamydospores of Hybrid 40 were reticulate.

TABLE 1.—*Pathogenicity of interspecies hybrids between Tilletia levis and T. tritici*

Parent or hybrid No.	Pedigree	Inoculum		Smut in—				
		Source	Generation	Hybrid 128	Oro	Albit	Hohenheimer	Hussar × Hohenheimer
				Percent	*Percent*	*Percent*	*Percent*	*Percent*
HYBRID L–8 × T–9								
L–8		Oro		90	85		0	
T–9		Hohenheimer		85	0		30	
35	L56–1 × T157–1 [1]	Hard Federation	F_2	26	12		0	
		Oro	F_3	82	70		0	
		do	F_4	81	84		0	
		do	F_5	84	77		0	
		do	F_6	92	85		0	
38	L56–1 × T157–4	Hard Federation	F_2	48	3		1	
		Oro	F_3	65	1		0	
		Hybrid 128	F_4	97	1		0	
		do	F_5	90	1		0	
		do	F_6	95	1		0	
39	L56–1 × T157–5	Hard Federation	F_2	94	33		21	
		Oro	F_3	85	30		27	
		Hohenheimer	F_3	90	27		33	
		Oro	F_4	88	24		22	
		Hohenheimer	F_4	89	28		32	
		Oro	F_5	86	28		26	
		Hohenheimer	F_5	79	30		35	
		Oro	F_6	87	84		20	
		Hohenheimer	F_6	96	72		68	
40	L56–1 × T157–8	Hard Federation	F_2	48	10		0	
		Oro	F_3	53	1		4	
		Hybrid 128	F_4	22	7		0	
		do	F_5	32	9		2	
		do	F_6	94	64		5	
HYBRID L–7 × T–10								
L–7		Albit		92		93	0	0
T–10		Hohenheimer		93		0	73	0
41	L70–2 × T67–3	Hohenheimer	F_2	70		0	0	0
		Hybrid 128	F_3	85			0	0
		do	F_4	87		1	0	0
42–1	L70–3 × T67–3	Hindi	F_1	30		1	0	0
		Hybrid 128	F_2	29		0	1	0
		do	F_3	98		0	0	0
42–2	do	Hybrid 128	F_2	96		95		
		Albit	F_3	92			0	0
		Hybrid 128	F_4	95		83	5	0
		Hindi	F_1	56		2	1	0
44	L71–1 × T69–1	Hohenheimer	F_2	47		1	2	0
		do	F_3	38			6	0
		do	F_4	10		1	7	0
46–1	L71–1 × T69–3	Hindi	F_1	27		3	1	0
		Albit	F_2	94		88	6	0
		do	F_3	86			0	0

[1] *T. levis* parent, chlamydospore 56, sporidium 1, crossed with *T. tritici* parent, chlamydospore 157, sporidium 1.

TABLE 1.—*Pathogenicity of interspecies hybrids between Tilletia levis and T. tritici*—Continued

HYBRID L-7 × T-10—Continued

Parent or hybrid No.	Pedigree	Inoculum: Source	Inoculum: Generation	Smut in—: Hybrid 128	Oro	Albit	Hohenheimer	Hussar × Hohenheimer
				Percent	*Percent*	*Percent*	*Percent*	*Percent*
46-2	L71-1 × T69-3	Hohenheimer	F_2	25		0	5	1
		do	F_3	33			3	1
		do	F_4	6		3	3	0
49	L71-2 × T69-2	Hindi	F_1	47		3	0	0
		Hybrid 128	F_2	78		8	4	0
		Hohenheimer	F_3	37			26	1
		do	F_4	7		0	1	0

HYBRID T-12 × L-8

T-12		Hohenheimer		92	1		67	
L-8		Oro		90	85		0	
67	T192-1 × L74-1	Hindi	F_1	75	7		7	
		Oro	F_2	86	36		6	
		do	F_3	88	82		15	
		Hohenheimer	F_2	81	16		61	
		do	F_3	77	14		74	
68	T192-1 × L74-2	Hindi	F_1	30	2		0	
		Hybrid 128	F_2	66	1		11	
		do	F_3	19	1		1	
73	T192-1 × L74-3	Hindi	F_1	63	5		18	
		Hohenheimer	F_2	81	12		29	
		do	F_3	63	1		27	

The relative pathogenicity of hybrids between races L–7 and T–10 is likewise presented in table 1. Albit and Hussar were susceptible to L–7 and resistant to T–10, whereas Hohenheimer was resistant to L–7 and susceptible to T–10. (The reaction of Hussar to these two races is not shown in table 1.) The variety Hussar × Hohenheimer (C. I. 10068–1) was highly resistant to both of these races as well as to all other known races of the wheat bunt fungi. This variety was selected from a cross between Hussar (C. I. 4843) and Hohenheimer (C. I. 11458). The primary purpose, therefore, in hybridizing L–7, which infects Hussar, and T–10, which infects Hohenheimer, was to test the theoretical possibility of obtaining segregates capable of infecting Hussar × Hohenheimer. It is apparent, however, from the data in table 1, that such segregates did not occur, since this variety was highly resistant to all the hybrids. Furthermore, most of the hybrids were less virulent than either of the parent races. For example, Hybrids 41 and 42–1 infected only the susceptible variety Hybrid 128. At least one other hybrid not included in table 1 gave a similar reaction. Hybrids 42–2 and 46–1 produced the same reaction as the L–7 parent, although, like the T–10 parent, the chlamydospores of both of the selections were reticulate. The remainder of the hybrids between L–7 and T–10 shown in table 1 infected Hybrid 128 only (except Hybrid 49, which produced 26 percent on Hohenheimer in the F_3), and this capacity appeared to decline in successive generations, especially when the inoculum was taken from Hohenheimer.

Data on the pathogenicity of hybrids between T–12 and L–8 are also presented in table 1. T–12 infects Hohenheimer but not Oro, whereas L–8 infects Oro but not Hohenheimer. Of the three hybrids studied, Hybrid 67 was the most virulent, being able to infect both Oro and Hohenheimer, whereas Hybrid 68 infected only Hybrid 128. Although it infected Hohenheimer, Hybrid 73 was less virulent on this variety than the T–12 parent. The chlamydospores of Hybrid 68 were smooth while those of the other two hybrids were reticulate.

RACE HYBRIDS

The data obtained from studies on hybrids between T–8 and T–9 are presented in table 2. Albit and Hussar are susceptible to T–8 and resistant to T–9, whereas Hohenheimer is resistant to T–8 and susceptible to T–9. As noted previously, Hussar × Hohenheimer is resistant to these and all other known races of *Tilletia tritici* and *T. levis*. It will be noted, however, that all the hybrids between T–8 and T–9 included in table 2, except Hybrid 53, were capable of infecting this variety. Three other hybrids between these races, not included in table 2, were similar to Hybrid 53 in their pathogenicity. In general, pathogenicity on Hussar × Hohenheimer was accompanied by greater virulence on Hohenheimer than that exhibited by the T–9 parent, and by less pathogenicity on Albit and Hussar than that exhibited by the T–8 parent. An exception to this may be noted in the case of Hybrid 56, which was more virulent on Hohenheimer and Albit than the parent races, though less virulent on Hussar than T–8. A preliminary report on the pathogenicity of hybrids between T–8 and T–9 and the transgressive inheritance of pathogenicity factors in some of these hybrids has been already made (*6*).

TABLE 2.—*Pathogenicity of interrace hybrids of Tilletia tritici*

HYBRID T-8 × T-9

Parent or hybrid No.	Pedigree	Inoculum		Smut in—				
		Source	Generation	Hybrid 128	Albit	Hohenheimer	Hussar × Hohenheimer	Hussar
				Percent	*Percent*	*Percent*	*Percent*	*Percent*
T–8		Albit		85	89	0	0	53
T–9		Hohenheimer		85	0	30	0	0
		Hindi	F_1	95	12	28	3	0
		Hussar × Hohenheimer	F_2	86		37	8	
		do	F_3	75		35	16	
		do	F_4	86	19	74	29	2
50	T60–1×T157–2 [1]	Hohenheimer	F_2	99	20	37	4	
		do	F_3	86		31	1	
		do	F_4	88	13	62	2	0
		Hybrid 128	F_2	94	13	0	0	
		Albit	F_2	94	83	0	0	
		Hindi	F_1	94	8	10	3	
52	T60–1×T157–4	Hussar × Hohenheimer	F_2	90		27	6	
		do	F_3	90		50	18	
		do	F_4	87	71	77	36	27
		Hindi	F_1	72	3	1	0	
53	T60–1×T157–5	Hybrid 128	F_2	63	1	0	0	
		do	F_3	74		1	0	
		do	F_4	23	1	1	0	0

[1] T–8 parent, chlamydospore 60, sporidium 1, crossed with T–9 parent, chlamydospore 157, sporidium 2.

TABLE 2.—*Pathogenicity of interrace hybrids of Tilletia tritici*—Continued

HYBRID T-8 × T-9—Continued

Parent or hybrid No.	Pedigree	Inoculum		Smut in—				
		Source	Generation	Hybrid 128	Albit	Hohenheimer	Hussar × Hohenheimer	Hussar
				Percent	*Percent*	*Percent*	*Percent*	*Percent*
54	T60-2×T157-1	Hindi	F_1	86	16	18	1	
		Hohenheimer	F_2	86	5	75	12	
		Hussar × Hohenheimer	F_3	95		20	13	
		do	F_4	92	20	67	37	3
55	T60-2×T157-2	Hindi	F_1	93	9	20	5	
		Hussar × Hohenheimer	F_2	92		36	19	
		do	F_3	89	30	85	56	7
		Hohenheimer	F_2	99	81	74	25	
		do	F_3	85		54	4	
		do	F_4	88	81	84	6	17
56	T60-2×T157-3	Hindi	F_1	93	12	24	2	
		Hussar × Hohenheimer	F_2	85		38	7	
		Albit	F_2	99	82	13	9	
		do	F_3	94		2	8	
		Hussar × Hohenheimer	F_4	94	85	89	44	29
		HYBRID T-8 × T-10						
T-8		Albit		85	89	0	0	93
T-10		Hohenheimer		93	0	73	0	0
61	T61-1×T67-1	Hindi	F_1	33			0	
		Hybrid 128	F_2	92	0	0	0	
		do	F_3	93		0	0	
		do	F_4	75	0	0	0	0
62	T61-1×T67-2	Hindi	F_1	91			3	
		Hussar × Hohenheimer	F_2	92		64	18	
		do	F_3	88		67	57	
		do	F_4	84	63	92	35	22
63	T61-1×T67-3	Hindi	F_1	83			0	
		Hybrid 128	F_2	30	0	0	0	
		do	F_3	78		0	0	
		do	F_4	95	4	0	0	0

Hybrids were also made between T–8 and T–10 to determine whether Hussar × Hohenheimer might be susceptible to any of the segregates. These races differ in the same manner as that described for T–8 and T–9. However, T–10 differs from T–9 by its greater virulence on Hohenheimer (7). The relative virulence of three hybrids between T–8 and T–10 is indicated by the data presented in table 2. Hybrids 61 and 63 were able to infect only Hybrid 128, whereas Hybrid 62 infected all of the varieties including Hussar × Hohenheimer, though it was less virulent on Hussar than the T–8 parent.

BACKCROSSES

Four backcrosses to the T–8 parent were made with two monosporidial lines from each of two chlamydospores from Hybrid 50 (T–8 × T–9). The virulence of these backcrosses is shown by the data presented in table 3, and it will be noted that Albit was highly susceptible to all of them as well as to the T–8 parent, whereas Hohenheimer exhibited varying degrees of susceptibility, depending upon the source of the inoculum (table 3).

TABLE 3.—*Pathogenicity of backcrosses of Hybrid 50 to the T–8 parent*

Parent and backcross No.	Pedigree	Inoculum		Smut in—		
		Source	Generation	Hybrid 128	Albit	Hohenheimer
				Percent	*Percent*	*Percent*
T–8		Albit		85	89	0
74	T60–1×H91–3[1]	Hindi	F_1	63	53	4
		Albit	F_2	76		21
		Hybrid 128	F_3	85	84	6
75	T60–1×H91–7	Hindi	F_1	90	75	31
		Hohenheimer	F_2	92		84
		do	F_3	87	80	82
		Albit	F_2	88		55
		Hybrid 128	F_3	94	93	17
76	T60–1×H92–1	Hindi	F_1	95	76	32
		Albit	F_2	85		19
		Hybrid 128	F_3	93	97	9
		Hohenheimer	F_2	91		80
		do	F_3	96	91	84
78	T60–1×H92–5	Hindi	F_1	76	81	14
		Albit	F_2	83		19
		Hybrid 128	F_3	91	93	40
		Hohenheimer	F_2	86		60
		do	F_3	94	79	73

[1] Chlamydospore 60, sporidium 1, of T–8, crossed with chlamydospore 91, sporidium 3, of Hybrid 50.

DISCUSSION

Hybridization has long been recognized as a possible factor in the origin of physiologic races of *Tilletia tritici* and *T. levis*. Although these species and their respective races can be hybridized readily under controlled conditions, the extent to which this process occurs under natural conditions is not known. Nevertheless it seems highly significant that many of the artificially produced hybrids have given rise to one or more new pathogenic types. In other words, the readiness with which this process functions under controlled conditions suggests that it probably occurs in nature at least occasionally. Furthermore, the results obtained from these studies tend to emphasize the possible importance of hybridization as a factor in perpetuating the bunt problem.

The importance of genetic factors in the basic inheritance of pathogenicity in the bunt fungi is evident from the data presented in the foregoing pages. However, the exact nature of this inheritance has not been determined, mainly because of the difficult, if not impossible task, of obtaining cultures of complete sets of primary sporidia from parent and hybrid chlamydospores.[5] Nevertheless, there appears to be sufficient evidence at hand to indicate that in hybrids involving differential reaction on two host varieties pathogenicity is inherited on at least a dihybrid basis. For example, at least three pathogenic types are represented by the four hybrids between L–8 and T–9 (table 1). Four pathogenic types would be expected where two factors are involved. These hybrids were produced by crossing one monosporidial line of L–8 with four monosporidial lines of T–9; two of the hybrids

[5] Hanna (*3*) perfected a technique which made it possible to obtain cultures of all the sporidia from a promycelium, but the method was not described.

are entirely different from both parents, whereas the other two appear to be the same as the L–8 parent. Therefore, at least three factor combinations appear to have occurred in these four hybrids. Similar results were obtained with hybrids between T–12 and L–8 (table 1).

Evidence of multiple factors and the extent to which new combinations of pathogenicity factors may occur in hybrids of the bunt fungi is indicated by results obtained with hybrids between T–8 and T–9 and T–8 and T–10 (table 2). Several of these hybrids produced segregates that were pathogenic on Hussar × Hohenheimer, a variety that is highly resistant to all known races of *Tilletia tritici* and *T. levis*. Apparently the dominant factor in the production of pathogenicity for Hussar × Hohenheimer was carried by certain sporidia of the T–9 parent. This is indicated by the pathogenic properties exhibited by Hybrids 50, 52, and 53. In pedigree, these hybrids differ only by the T–9 parent, and the fact that Hybrid 53 was nonpathogenic on Hussar × Hohenheimer suggests that sporidium 5 of the T–9 parent lacked the factor or factors necessary to produce pathogenicity on this variety. Similarly the results obtained with Hybrids 50 and 55 suggest a dominant influence of the T–8 parent on the reaction of Albit. The pedigree of these hybrids differs on the side of the T–8 parent, and segregates of Hybrid 55 that were highly virulent on Hohenheimer and Hussar × Hohenheimer were more virulent on Albit than similar segregates of Hybrid 50. In other words, the factor or factors for virulence on Albit in sporidium 1 of the T–8 parent were different from those in sporidium 2. Furthermore, the greater susceptibility of Hohenheimer to certain segregates of Hybrids 50 and 55 than to the T–9 parent suggests that the T–8 parent contributed to the virulence of these segregates on this variety.

The high virulence on Hohenheimer exhibited by Hybrid 50 was evident also in backcrosses of this hybrid to the T–8 parent (table 3). Three of the backcrosses were more virulent on Hohenheimer than the T–9 parent, and they were equally as virulent on Albit as the T–8 parent. Furthermore, it seems probable that the other backcross (Hybrid 74) would also have been highly virulent on Hohenheimer, if the inoculum had been taken from that variety.

Although pathogenicity in *Tilletia tritici* and *T. levis* apparently is controlled by genetic factors, the selective influence of the host variety plays an important part in the expression of pathogenic properties and hence in the establishment of new physiologic races. Evidence of this is shown by the results obtained with several of the hybrids used in these studies. For example, the repeated selection of inoculum of Hybrid 39 (table 1) from Oro through the sixth generation resulted in a marked increase in virulence on Oro with no change in virulence on Hohenheimer, whereas the selection of the inoculum of this hybrid from Hohenheimer resulted in an increase in virulence on both Oro and Hohenheimer. In contrast, a marked decrease in virulence was exhibited by Hybrids 46 and 49 (table 1), even on the susceptible variety Hybrid 128, when the inoculum was repeatedly taken from Hohenheimer. The influence of host selection on pathogenicity is further indicated by the infection of Hussar × Hohenheimer by hybrids between T–8 and T–9 (table 2). The inoculum that was taken repeatedly from Hussar × Hohenheimer increased in virulence on this variety, whereas selections of the same hybrids taken from

other varieties decreased in virulence on Hussar × Hohenheimer. Similar results were obtained with other hybrids (table 2).

Independent inheritance of factors for pathogenicity, and for spore morphology, is indicated by the results obtained with Hybrids 42–2 and 46–1 (table 1). Both of these hybrid segregates possessed the pathogenicity of the L–7 parent and the spore morphology of the T–10 parent.

SUMMARY

The results from investigations on 50 interspecies and interrace hybrids of *Tilletia tritici* and *T. levis* are presented. Approximately 83 percent of the interspecies hybrids perpetuated themselves, in contrast to only 59 percent of the interrace hybrids. On the other hand, the race hybrids were more productive of new pathogenic segregates than the species hybrids.

Some of the segregates from the various hybrids were more virulent than the parent races, others were less virulent, while still others were similar in pathogenicity to the parent races.

Entirely new combinations of pathogenicity factors were produced in several of the hybrids, as indicated by their pathogenicity on the variety Hussar × Hohenheimer, which is highly resistant to all known naturally occurring races of the wheat bunt fungi.

Pathogenicity in *Tilletia tritici* and *T. levis* is genetically controlled and apparently inherited on a multiple-factor basis. Factors for pathogenicity and spore morphology are inherited independently.

The selective influence of the host variety is important in the establishment of new pathogenic types resulting from hybridization.

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